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Generalist ground-nesting bees dominate diversity survey in intensively managed agricultural land

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Abstract. In Western Europe agricultural management was intensified in the period 1950–2010 with negative consequences for ecosystem services, such as pollination, especially in countries with a large proportion of agriculture. Farmland represents 66% of the Danish landscape, but little is known about wild bees despite that 75% of the country's wild and cultivated plant species depend on insect pollination. Strawberry (*Fragaria* × *ananassa*) gains considerable benefits from insect pollination and abundance, species richness and functional diversity, are all important elements. We surveyed the diversity of wild bees during strawberry flowering by sampling bees with pan-traps along permanent margins bordering strawberry fields on six organic and six conventional farms in eastern Denmark and compared the results of the survey with that of sampling site farming practice and field margin forage availability. The majority of bees sampled were polylectic solitary ground-nesting bees known to forage on species of the rose family. This indicates that these bee species are potential pollinators of strawberries, and the low number of specialized bees suggests that the bee community was affected by the simplified landscapes. Temporal trends in abundance, species richness, and body size of the bees, suggest that the functional diversity of pollinator assemblages available differed for early- and late-flowering strawberries. Fewer plants species and a lower plant cover were found in the margins of sprayed fields. Abundance and diversity of the wild bees were neither correlated with the use of herbicides and insecticides, nor with plant species richness or flowering plant cover.

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INTRODUCTION

Agricultural management has over the past 60 years been intensified with more use of pesticides and increasing size of crop fields, which has reduced and fragmented semi-natural habitats and caused a severe reduction in biodiversity of agricultural land (Benton *et al*., 2003; Bianchi *et al*., 2006). The agricultural value of wild bees is their contribution to crop pollination and studies have shown that abundance, species richness and functional diversity of bees can increase yield and quality of flowering crops (Garibaldi *et al*., 2013; Slaa *et al*., 2006; Winfree *et al*., 2008). Among other factors, the functional diversity of wild bees can depend on interspecific differences in bee body size. Bee body size affect important pollinator traits such as within flower behavior (Barrow & Pickard, 1984; Hoehn *et al*., 2008; Stout, 2000), foraging range (Gathmann & Tscharntke, 2002; Walther-Hellwig & Frankl, 2000), and activity level at lower temperatures (Heinrich & Heinrich, 1983; Heinrich, 2004; Stone & Willmer, 1989). Functional diversity also increases with species richness of the bees present. However, diversity of wild bees is vulnerable to agricultural intensification (Kells & Goulson, 2003; Osgathorpe *et al*., 2012; Steffan-Dewenter & Tscharntke, 1999), and farming practice can impact on species diversity. Organic farms generally have smaller field sizes and more semi-natural habitat than conventional farms and support more plant species than farms where pesticides are applied (Aude *et al*., 2004; Norton *et al*., 2009; Petersen *et al*., 2006). The same pattern has been found concerning bee diversity and abundance with organic farms having a higher species diversity of wild bees than conventional ones (Ekroos *et al*., 2008; Holzschuh *et al*., 2008; Karanja *et al*., 2010).

The negative impact of intensified agriculture might be particularly strong in countries with a large proportion of arable fields. Farmland represents 66% of the Danish landscape (Statistics Denmark, 2014) which means that in the intensely managed agricultural landscape of Denmark, farming systems and permanent field margins, and the resources they offer, may significantly influence the overall biodiversity. Bumble bee species and numbers have declined in Denmark (Dupont *et al*., 2011), but although 75% of wild and cultivated plant species require insect pollination (Holm, 1982; Prip *et al*., 1996), there is little knowledge about wild bees on agricultural land in this country (Ahrenfeldt *et al*., 2015; Calabuig, 2000; Henriksen & Langer, 2013). The current study helps fill this gap.

Strawberry (*Fragaria* × *ananassa*) was chosen as a focal crop as it gains considerable benefits from insect pollination. Bee abundance, bee species richness, and interspecific differences in bee body sizes all positively affect fruit weight and number of fully developed marketable fruits, their sweetness, and shelf life (Chagnon *et al*., 1989; Chen *et al*., 2011; Klatt *et al*., 2014; Nye & Anderson, 1974). We paired organic and conventional farms in eastern Denmark and collected wild bees in the margins of strawberry fields throughout strawberry flowering in order to investigate possible changes in the bee community during this time, and to analyze response of bee diversity to pesticide use and flower availability in the permanent margins surrounding the study fields.

We hypothesized that: 1) The composition of body sizes of the wild bee community would change throughout strawberry flowering with the appearance of more bumblebees in early summer; and 2) Wild bee activity-density — in this study used as a more accurate descriptor of abundance — and species richness would be positively affected by availability of flowering plants in the permanent margins of the strawberry field, and negatively by the use of herbicides and insecticides.

MATERIALS AND METHODS

Study fields: Six conventional and six organic strawberry fields on Zealand (eastern Denmark) were selected for this study. Farms were paired geographically in conventional and organic farms, as far as possible, to minimize an interaction between landscape and farming practice. Selected fields had the strawberry cultivar 'Honeoye', and all fields but one had a bordering hedge running along the longest side of the field. One organic field did not have a bordering hedge, and thus a hedge bordering a nearby pond was chosen for trap placement. The study fields were situated at least 600m apart. Initial analysis showed that conventional fields differed in pesticide use, and thus they were divided into two categories, *i.e.*, 'high-' and 'low-intensity farming'. High-intensity fields were the four conventional fields treated with herbicides, insecticides and fungicides, and low-intensity fields were two conventional ones only treated with fungicides, and six organic fields (Table 1). Herbicides were applied on all conventional farms before establishing new strawberry plants — after harvest when the previous strawberry plants were removed from the field.

Sampling of bees: Five traps, positioned at strawberry flower height, were placed along the hedge margin facing the strawberry field at approximately the middle of the field. Traps were white plastic bowls mounted on a wooden pole, and trap fluid consisted of 1/3 ethylene glycol, 2/3 water, and a drop of detergent. Trap catches were collected four times in 2010, from late May through early and middle June to late June, and each time traps were active for ten consecutive days, resulting in 40 days of continuous sampling. We use the term "sampling period" to convey the four separate periods trap catches were collected: late May, early June, middle June, and late June. The likelihood of an insect being trapped is a function of trap diameter and color, its activity, and species abundance (Obrist & Duelli, 2010). The number of bee individuals sampled in pan traps thus represents bee 'activity-density' during sampling, and thus this term will be used subsequently to describe bee abundance. We trapped honey bees (*Apis mellifera* Linnaeus) but we did not include them in our analysis or counts of individuals and species.

Floral survey: Floral surveys were conducted both at field margins and within the study fields. Surveys were done along all semi-natural herbaceous margins and in the hedge sites where the traps were established. Additional hedges around the field were not surveyed, because they were similar to the surveyed hedge sites. Each vegetation survey was done within six plots of 2.0m × 0.5m on each side of the pan traps, or the equivalent position in margins without traps. There was a minimum distance of 5m between plots. Plant species numbers and plant cover, excluding grasses, was surveyed. For the hedge survey (2.0m × 0.5m on each side of the pan traps) and the vegetation survey in the field only species numbers were noted. Vegetation surveys within the field consisted of nine plots of 2.0m × 0.5m spread randomly over the field. Additionally, the proportion (cover) of strawberry plants in bloom was estimated for the whole field when traps were filled and emptied.

Data analysis: We used three different models to analyze the effects on three different response factors: 1) activity-density of all wild bees sampled, 2) activity-density of individuals from the most abundant genus, *Andrena* Fabricius (Andrenidae); and 3) overall wild bee species richness. We tested the effect on wild bees of the following fixed factors in all three models: farming intensity, the cover of flowering plants in the field margins, plant species richness in the field and field margins, the abundance of strawberry flowers, and sampling period. In all three models we used a Poisson mixed effects model. Due to some traps being inactive (damaged in one way or another) during sampling period, we used the number of traps as an offset in the Poisson model to

Table 1. Characteristics of the study sites. Strawberry farms sampled with farming practice and intensity, field identity, locality, geographical UTM coordinates (Zealand includes zones 32 and 33; we used the modified map where all of Zealand is in zone 32), number of wild plant species in and around fields, average cover of plants in permanent margins surrounding the field, effect of farming intensity on number of plant species, and cover of plants and bare soil. High-intensity fields were treated with herbicides and insecticides, and low-intensity fields were either treated only with fungicides or had organic management. Plant cover was significantly higher around low intensity fields (t-test, $p < 0.05$), and there was a tendency for higher numbers of wild plant species in and around low-intensity fields (standard Poisson regression model, $p = 0.079$).

Farming practice	Farming intensity*	Field #	Locality	UTM-East	UTM-North	Plant species	Plant cover (%)
Conventional	High	C1	L. Skensved	700412	6159759	32	51
		C3	Ringsted	678907	615417	40	54
		C4	Slagelse	647026	6143613	19	19
		C5	Skælskør	648014	6127775	22	52
	Averages high (mean ± SD)					28 ± 10	44 ± 17
	Low	C2	Ruds Vedby	653840	6159015	38	73
		C6	Klippinge	710005	6139644	47	74
Organic		O1	Lejre	687451	6166198	32	78
		O2	Fjenneslev	670332	6146341	24	63
		O3	Klippinge	710043	6140360	44	58
		O4	Skælskør	650313	6129770	28	76
		O5	Ringsted.	669561	6151293	36	85
		O6	L. Skensved	697890	6157065	26	44
	Averages low (mean ± SD)					34 ± 8	69 ± 13

*Fungicides were applied on all conventional fields 1–5 times every year. Herbicides were applied on all conventional farms, after harvest, the year previous strawberry plants were removed from the field. On high-intensity farms herbicides were also applied during the non-harvest years, *i.e.*, when strawberry plants were established in the field; insecticides were applied on high-intensity farms 2–4 times a year.

adjust for the count of bees. For all pairwise comparisons of means, Tukey tests were used. For each analysis auto-correlation within farms and over time was taken into account as two separate random effects. Strawberry flowering was calculated as the average proportion of strawberry flowers open at the beginning and end of a given bee trapping period. Model reduction was performed on the fixed effects, and neither of the random effects were tested for significance. To describe the effect of farming intensity on plant cover vegetation in field margins we used a one-way ANOVA with two levels ('high intensity', 'low intensity'). All statistical analyses were performed using R version 3.1.2 (R Development Core Team, 2012).

RESULTS

Survey results: In total, 701 wild bee specimens were sampled, these represented 41 species from seven genera (Table 2); 611 individuals were from 32 polylectic species of which many forage on plants from the family Rosaceae, to which strawberries belong (Bees, Wasps & Ants Recording Society, 2014; Martin, 2014). The large majority of bee species and individuals were soil-nesting solitary bees (*Andrena* spp., *Halictus* spp., and *Lasioglossum* spp.: Michener, 2000), with *Andrena* spp. being by far the most abundant and species-rich group. Cavity-nesting solitary bees were rare, with two species and six individuals sampled (*Osmia* spp. and *Chelostoma* spp.: Michener, 2000), as were bumble bees (Apidae) that were represented by 27 individuals and 8 species.

Effect of sampling period, farming intensity, and forage resources: Sampling period (*i.e.*, the sampling period between catch collection when traps were active) was the only tested factor to have a significant effect on the responses in the three models: activity-density on all individuals (final model: $F_{(3, 42)}$=18.89, p<0.001), activity-density of *Andrena* spp. (final model: $F_{(3, 42)}$=16,77, p<0.001), and species richness (final model: $F_{(3, 42)}$=20.01, p<0.001), with more individuals and species observed in late May and late June compared to the two other sampling periods in early and middle June (Figs. 1, 2). Overall wild bee activity-density was not significantly affected by farming intensity (full model z-test: z=-0.619, p =0.536), plant species richness (full model z-test: z=1.230, p=0.219), flowering plant cover (full model z-test: z=-0.558, p=0.577), or abundance of strawberry flowers (full model z-test: z=-0.496, p=0.620). Wild bee species richness likewise was not significantly affected by farming intensity (full model z-test: z=-0.722, p=0.470), plant species richness (full model z-test: z=1.167, p=0.243), flowering plant cover (full model z-test: z=-0.222, p=0.824), or abundance of strawberry flowers (full model z-test: z=-0.582, p=0.56). Finally, no significant effect of the remaining factors was found on activity-density of *Andrena* spp.: farming intensity (full model z-test: z=-0.424, p=0.672), plant species richness (full model z-test: z=0.476, p=0.634), flowering plant cover (full model z-test: z=-0.316, p=0.752), or abundance of strawberry flowers (full model z-test: z=-0.520, p=0.603).

Effect of farming intensity on field margin resources: Farming intensity had a significant effect on flowering plant cover (t-test: t=-2.84, p=0.018) (Table 1). There was a tendency for plant species richness to be higher in low intensity fields and field margins compared to high intensity fields (z-test: z=1.76, p=0.079).

DISCUSSION

Seasonal trends in wild bee activity-density and species richness: Bee activity-density and species richness were highest in late May and late June with a lower cap-

Table 2. Total number of wild bees and bumble bees collected in pan traps from late May to late June 2010 in the margin of 12 strawberry fields. Floral specialization has been included (Martin, 2014). High-intensity sites were four conventional strawberry fields treated with herbicides and insecticides, while low-intensity sites were six organic fields and two conventional ones only treated with fungicides.

Wild bees	**High intensity**	**Low intensity**	**Total bees**	**Floral relationship**
Andrena bicolor	0	1	1	polylectic+
A. carantonica	22	23	45	polylectic+
A. chrysosceles	0	1	1	polylectic+
A. cineraria	1	3	4	polylectic+
A. fucata	1	0	1	polylectic+
A. fulva	1	9	10	polylectic+
A. haemorrhoa	50	230	280	polylectic+
A. helvola	29	92	121	polylectic+
A. minutula	0	4	4	polylectic+
A. minutuloides	2	2	4	polylectic
A. nigroaenea	25	42	67	polylectic+
A. nitida	1	0	1	polylectic+
A. praecox	0	21	21	oligolectic (*Salix* spp.)
A. semilaevis	0	6	6	polylectic
A. subopaca	2	3	5	polylectic+
A. tibialis	2	1	3	polylectic+
A. wilkella	0	3	3	oligolectic (Fabaceae spp.)
Total *Andrena* spp.	**136**	**441**	**577**	
Bombus cryptarum	0	2	2	polylectic
B. hortorum	0	1	1	polylectic
B. hypnorum	1	3	4	polylectic
B. lapidarius	1	1	2	polylectic
B. lucorum	3	3	6	polylectic+
B. pascuorum	2	1	3	polylectic+
B. pratorum	1	4	5	polylectic+
B. terrestris	3	4	7	polylectic+
Total *Bombus* spp.	**11**	**19**	**30**	

ture in the two sampling periods in early and middle June (Figs. 1, 2). The two peaks in both activity-density and species richness correspond with early solitary bee species peaking in activity in late May and bumble bee workers from various species emerging in middle June. Both bumble bees and solitary bees have been found capable of switching between habitats — foraging where plant species richness and abundance are highest at a given time during the season (Carvell *et al.*, 2007; Mandelik *et al.*, 2012). It is possible that the dearth of individuals and species found in early and middle June

Table 2. Continued.

Wild bees	High intensity	Low intensity	Total bees	Floral relationship
Halictus tumulorum	2	2	4	polylectic+
Lasioglossum albipes	8	0	8	polylectic+
L. calceatum	0	8	8	polylectic+
L. leucopus	0	4	4	polylectic
L. minutissimum	0	1	1	polylectic
L. parvulum	1	0	1	polylectic+
L. punctatissimum	0	1	1	polylectic+
L. quadrinotatum	0	1	1	polylectic
Total *Lasioglossum* & *Halictus* spp.	**11**	**17**	**28**	
Nomada fabriciana	0	2	2	—
N. ferruginata	0	1	1	—
N. flavoguttata	0	2	2	—
N. marshamella	3	3	6	—
N. panzeri	5	44	49	—
Total *Nomada* spp.	**8**	**52**	**60**	
Osmia bicornis	0	5	5	polylectic+
Chelostoma florisomnis	0	1	1	oligolectic (Ranunculaceae spp.)
Total *Osmia* spp. & *Chelostoma* spp.	**0**	**6**	**6**	
Total bees	**166**	**535**	**701**	
Total species	**22**	**36**	**40**	

* Polylectic: bees foraging in several plant families; polylectic+: bees foraging in several families and known to forage on Rosaceae; oligolectic: bees foraging within one plant family; — parasitic bees.

was also due to other habitats offering the polylectic bees better forage. The ability to use the resources from different plant families make polylectic bees less vulnerable to landscape fragmentation than oligolectic bees that are restricted to one plant family or sometimes only a few species of plants (Steffan-Dewenter *et al*., 2006). The high proportion of polylectic bees found in this study suggests that an adaptation to a fragmented agricultural landscape with the associated loss of oligolectic bees may have taken place.

The majority of individuals and species sampled in this study were polylectic and known to forage in Rosaceae, which indicates that these bees are potential pollinators of strawberry (Table 2). Strawberries require many individuals, species and bees of different sizes in order to develop optimally (Chagnon *et al*., 1989, 1993; Klatt *et al*., 2014). A previous study of pollinators in strawberry fields showed that wild bee species richness was lower in the field middle than closer to field margins (Ahrenfeldt *et al*., 2015). The current study found that wild bee activity-density and species richness changed during 40 days in spring and early summer which may have had a negative effect on pollination of cultivars flowering in early June and middle June when both

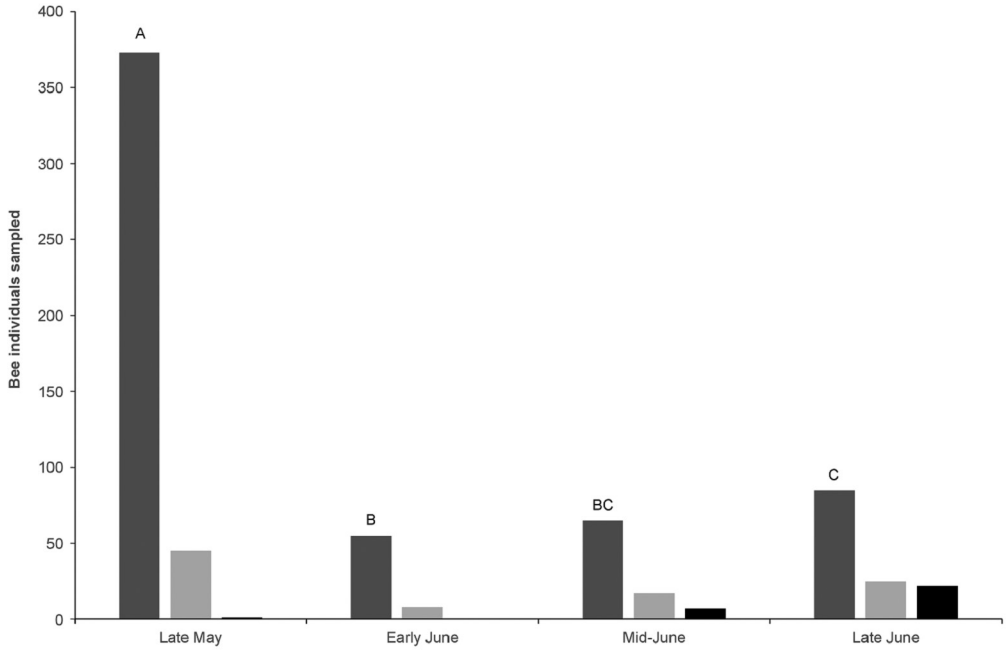

Figure 1. Total number of bees sampled in this study at the four different sampling periods. Dark grey bars: individuals from the genus *Andrena* Fabricius (Andrenidae); light grey bars: individuals from the genera: *Halictus* Latreille, *Lasioglossum* Curtis (Halictidae), *Osmia* Panzer (Megachilidae), and *Nomada* Scopoli (Apidae); black bars: individuals from the genus *Bombus* Latreille (Apidae). Different letters above the dark grey bars indicate a significant statistical difference between sampling periods in activity-density of individuals from all sampled genera ($F_{(3, 42)} = 18.89$, $p < 0.001$).

parameters were low. Furthermore, the presence of bumble bees and thus large-bodied bees increased towards late June, which means size differences between species increased. Bee body size affect within-flower pollinator behavior and optimal strawberry development depends on a variation in body sizes. In addition, larger bodied bees have larger foraging ranges and higher activity rates during lower temperatures. Changes in the functional diversity of pollinator assemblages throughout strawberry flowering may affect pollination services of specific strawberry cultivars during the year, depending on their peak flowering time and also between years, depending on field sizes, and weather conditions.

NO EFFECT OF FIELD MARGIN RESOURCES OR FARMING INTENSITY ON WILD BEES: Plant species richness and flowering plant cover in the strawberry field margins had no effect on overall activity-density of wild bees and species richness or on the activity-density of *Andrena* spp. Wild bees often fly along linear features such as hedges to orient themselves in the landscape (Calabuig, 2000), and our results suggest that the bees sampled did not rely extensively on the resources available within the field or field margins bordering the traps. Some of the bees may have been trapped flying along the hedge from one location of resources to another rather than foraging in the field margins bordering the strawberry field. This is supported by the fact that abundance of strawberry flowers in the individual fields had no effect on wild bee diversity.

Farming intensity did not have significant effect on any of the measures of bee diversity. The majority of all bees sampled in this study were solitary bees, which support research that shows that solitary bees are not affected by local farming practice

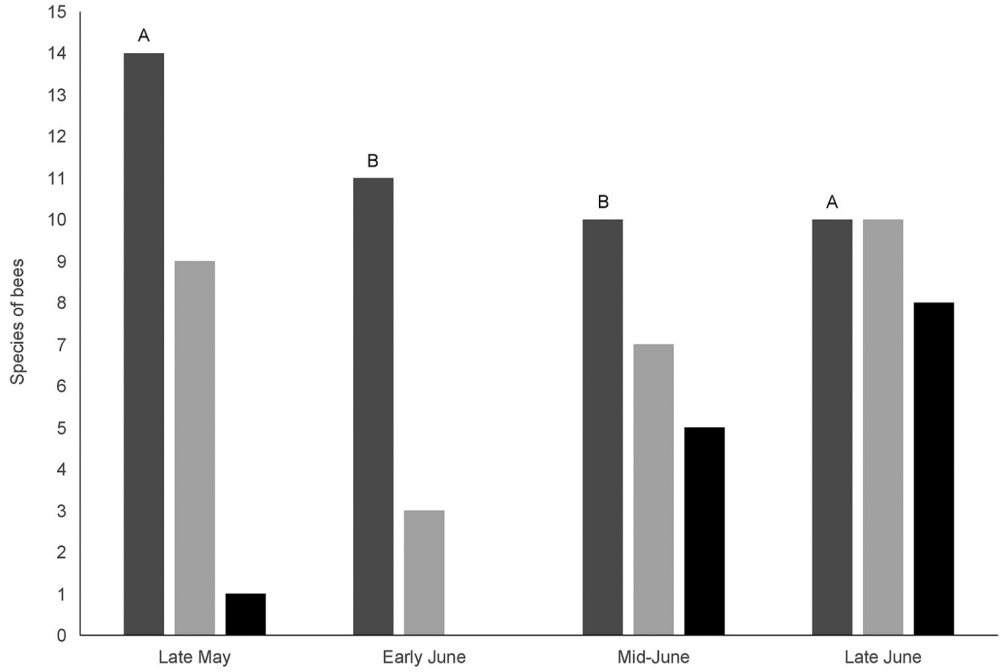

Figure 2. Species richness compared between sampling periods. Dark grey bars: species from the genus *Andrena* Fabricius (Andrenidae); light grey bars: species from the genera: *Halictus* Latreille, *Lasioglossum* Curtis (Halictidae), *Osmia* Panzer (Megachilidae), and *Nomada* Scopoli (Apidae); black bars: species from the genus *Bombus* Latreille (Apidae). Different letters above the dark grey bars indicate a significant statistical difference between sampling periods in total species richness of all sampled genera ($F_{(3, 42)} = 20.01$, $p < 0.001$).

(Gabriel *et al*., 2010). However, high intensity fields were treated with herbicides the year strawberry plants were established in the field and not during the three harvest years. Insecticides were applied 2–4 times a year. The difference in pesticide use between high- and low-intensity farms may thus have been too low to differentially affect bees.

Effect of farming intensity on field margin resources: Use of herbicides negatively affected the abundance of flowering plants and flowering plant species richness (Table 1). This result has been found in several other studies that report higher abundance and species richness of local wild plants in organic compared to conventional farming — with the use of pesticides and fertilizer as the main negative effect (Aude *et al*., 2003; Gabriel *et al*., 2010; Petersen *et al*., 2006). Thus, although flowering plants in both hedge, field margin, and within the field were affected by farming intensity this did not translate directly to an effect on wild bees in this study.

CONCLUSION

The majority of bees sampled in this study were polylectic species known to forage in Rosaceae which indicate that these bees are potential pollinators of strawberry. However, due to changes over time in activity-density, species richness, and body

size of bees sampled, the functional diversity of pollinator assemblages, and thus the pollination service available may differ for early- and late-flowering strawberries. Furthermore, the high proportion of polylectic bees found in this study suggests that an adaptation to a fragmented agricultural landscape with the associated loss of oligolectic bees may have taken place. Adaptation to fragmented resources may also explain why the bee communities were not affected by farm level intensity or the abundance and species richness of plants in immediate proximity of the sampling site, despite plants being negatively affected by farming intensity. It is possible that a landscape level survey of resources and farming intensity had shown an effect on wild bee abundance and diversity.

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